ERYTHRINA OLIVIAE: A NEW CASE OF ORIOLE POLLINATION IN MEXICO[1]

VÍCTOR MANUEL TOLEDO[2] AND HÉCTOR M. HERNÁNDEZ[2]

ABSTRACT

Erythrina oliviae, a dry-season-flowering tree from Mexico, is primarily pollinated by perching passerine birds. Other pollinators have also been noted. The nontubular flowers are directed to the ground, and the keel and wings function as nectar containers. The perch is vertical. The flowers produce large amounts of nectar, which contains a low percentage of sugar and a high number of amino acids.

It is possible to recognize two basic patterns in the flower structure of genus *Erythrina* (Leguminosae): (1) the standard enormously elongated and the keel and wings reduced to minimal size, and (2) the standard ovate or obovate and the keel and wings more or less conspicuously exserted from the calyx. In the first case the flower takes a decidedly tubular shape, and in the second it assumes a more generalized gaping configuration. A general correlation between these flower structures and pollination types may be also assumed. In the first case, the flowers can apparently be visited and pollinated efficiently only by hummingbirds,[3] and all the species, except the small African sect. *Humeanae* Barneby & Krukoff, with this kind of flower are from the New World (Raven, 1974, 1977; Toledo, 1974). In the second case the flowers are generally adapted to perching-bird pollination (Docters van Leeuwen, 1932; Singh, 1929; Ali, 1932), although they are also visited by hummingbirds, insects, squirrels and bats (Raven, 1977) and are predominantly, but not exclusively, from the Old World. In fact, a review of Krukoff & Barneby's (1974) conspectus of *Erythrina* shows that although the majority of American species (55) have tubular flowers and are therefore hummingbird pollinated, there are also a few species (12) with more generalized flowers (Table 1). The studies of pollination biology in this second group of species are very relevant because in it are included the species of subgen. *Micropteryx*, which has been considered the most primitive of the genus, and therefore perching-bird pollination in America may be considered an archaic syndrome which apparently preceded pollination by hummingbirds. At present, the data that have appeared about the pollination of American species of *Erythrina* with nontubular flowers seem to indicate that in this group both passerine bird pollination and hummingbird pollination is possible. They suggest

---

[1] We are grateful to M. Sousa for providing information about the species studied. We wish to thank M. Campomanes for amino acids analysis of nectar, L. Herrera who made the illustrations, and Alfonso Delgado for reading the manuscript. Finally we are especially grateful to Dr. Peter H. Raven for encouragement and for providing information, and Dr. Rupert Barneby for critically reading the manuscript.

[2] Instituto de Biología, Universidad Nacional Autónoma de México, Apdo. 70-233, México 20, D. F., Mexico.

[3] The following may be an exception; although van der Pijl (1937) proposed a possible disharmony between Asiatic flower-birds and American bird-flowers, Doctors van Leeuwen (1932; 93) refers to the case of the Venezuelan *Erythrina* (*E. umbrosa* H.B.K. which is a synonym of *E. mitis* Jacquin) which is cultivated in Java and visited by three species of sunbirds.

ANN. MISSOURI BOT. GARD. 66: 503–511. 1979.

0026-6493/79/0503–0511/$1.05/0

TABLE 1. American species of *Erythrina* with nontubular flowers.

Taxon	Distribution
Subgen. *Micropteryx* (Walpers) J. G. Baker	
E. fusca Loureiro	Pantropical
E. crista-galli L.	Uruguay, Argentina, Paraguay, Brazil, Bolivia
E. falcata Bentham	Argentina, Paraguay, Brazil, Bolivia, Peru
E. poeppigiana (Walpers) O. F. Cook	Bolivia, Brazil, Peru, Ecuador, Colombia, Panama
E. verna Velloso	Brazil, Bolivia
E. ulei Harms	Brazil, Bolivia, Ecuador
E. dominguezii Hassler	Brazil, Paraguay, Bolivia, Argentina
Subgen. *Erythrina*	
E. breviflora A. DC.	Mexico
E. edulis Triana	Peru, Colombia, Ecuador, Venezuela
E. oliviae Krukoff	Mexico
Subgen. *Erythraster* Barneby & Krukoff	
E. velutina Willd.	Brazil, Ecuador, Colombia, Venezuela, Antilles
E. grisebachii Urban	Cuba

that pollination by hummingbirds in *Erythrina* is not limited to tubular flowers. Thus, the studies by M. Duncan in *E. fusca* (Raven, 1974) and in *E. breviflora* (Cruden & Toledo, 1977) have demonstrated that the flowers of these species are visited and pollinated by orioles and other passerine birds. In *E. poeppigiana*, on the other hand, hummingbirds are frequent (Snow & Snow, 1972; Raven, 1977), although the primary visitors are orioles and other perching birds (Skutch, 1954; Snow & Snow, 1971; Timkin, 1970; Feinsinger et al., this symposium). Finally, some casual reports (Stiles, 1973; Pickens, 1931) indicate that *E. crista-galli* is visited at times and apparently pollinated by hummingbirds. In this paper, the pollination of another American species of *Erythrina* with nontubular flowers is described and discussed: *E. oliviae*. The voucher for this species (*H. M. Hernández 2*), as well as other vouchers for species mentioned in this paper, were verified by B. A. Krukoff and are deposited at MEXU and NY.

STUDY SITES AND METHODS

Erythrina oliviae is a tree endemic to central Mexico where it has been collected only in restricted areas of the Río Balsas depression. This species is called "zompantle," and occurs particularly along the streams of pronounced slopes. Flower visitors and their behavior were studied in April and May of 1978 in three localities: El Papayo (between Izúcar de Matamoros and Acatlán) and Chinantla, both in Puebla, and Infiernillo in Michoacán (Fig. 1A). The two first localities are situated in the easternmost portion of the depression (high Balsas), while the third is on the west of it (low Balsas). All the sites have a very dry and hot climate, with an annual precipitation between 650 (Acatlán) and 490 mm (Infiernillo) and an annual average temperature between 24.6 (Acatlán) and 29.6°C (Infiernillo). There is a pronounced dry season from

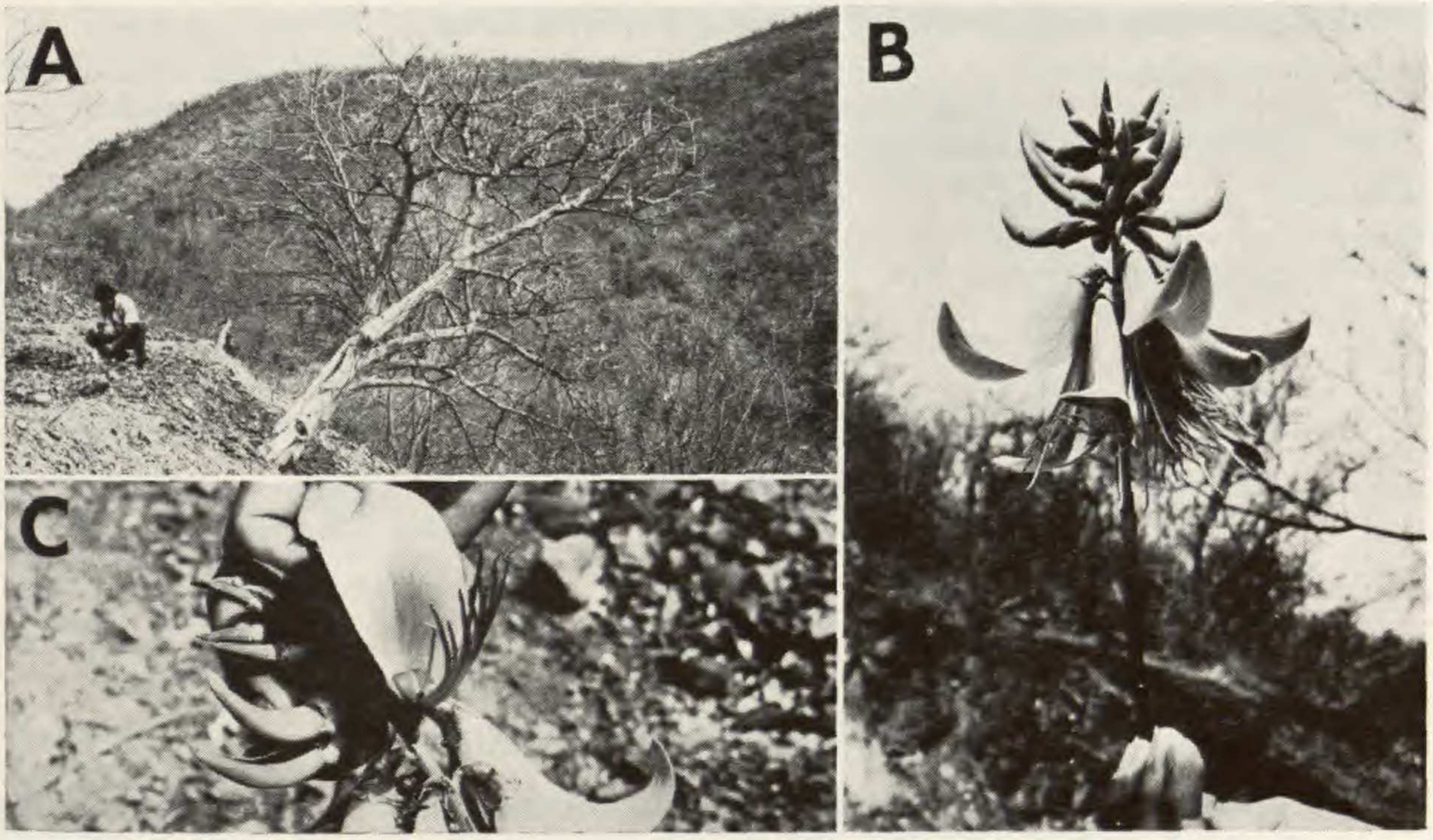

FIGURE 1. *Erythrina oliviae*.—A. A tree in the Infiernillo region.—B. Inflorescence.—C. Flower showing the sexual parts. Note the form of the keel and wings.

November to mid-May. All the sites are covered by tropical dry forests, with plants such as *Bursera* spp., *Pseudosmodingium perniciosum* (H.B.K.) Engler, *Ceiba parvifolia* Rose, *Lysiloma microphylla* Bentham, *Ipomoea* spp., *Pithecellobium dulce* (Roxb.) Bentham, *Prosopis juliflora* (Swartz) A. DC., and cacti such as *Lemairocereus*, *Cephalocereus* and *Myrtillocactus* (Miranda, 1947).

Nectar volumes were measured with calibrated micropipets and sugar concentrations with an Erma Hand Refractometer. The identification of amino acids in the nectar was made by M. Campomanes of Instituto de Investigaciones Biomédicas, UNAM, using an Aminco Flourometric Liquid Chromatography System. The nectar was removed from several flowers with a sterilized syringe and immediately refrigerated. Only nectar from the El Papayo population was taken for the amino acids identification.

FLOWERING TIME AND FLOWER CHARACTERISTICS

Like many other species of *Erythrina*, *E. oliviae* flowers towards the last part of the dry season (mid-April to mid-June). The inflorescence is an erect raceme 20–30 cm long (Fig. 1B). Each inflorescence has from 40 to 80 flowers which are directed downwards. The standard is very large (9 cm long × 3 cm wide when open) and of a bright to pale orange color; the very reduced keel and wings form a compact concavity for the nectar and are colored bright reddish orange (Fig. 1C). The stamens are arranged in three ranks of different length, and the pistil lies in the center of them. This species is very noticeable from long distances when it is in bloom. An estimate made in a tree at Infiernillo gave a total of 350 inflorescences.

TABLE 2. Some characteristics of nectar of *Erythrina oliviae*.

Flower	High Balsas (El Papayo, Puebla)		Low Balsas (Infiernillo, Michoacán)	
	μl/flower	% Sugar/ flower	μl/flower	% Sugar/ flower
I	220	11.74	170	11.32
II	230	11.68	210	11.40
III	260	11.76	270	11.40
IV	250	12.03	260	11.57
V	230	11.72	100	11.57
VI	225	11.60	280	10.77
VII	220	11.56	270	10.77
	x̄ 233.5	11.72	222.8	11.30

NECTAR PRODUCTION AND CONSTITUENTS

The analysis of nectar sampled for two populations of *Erythrina oliviae*, one in the high Balsas and the other in the low Balsas (Table 2), shows that the flowers produce extremely large volumes of nectar with a low percentage of sugar. It is interesting that the results are very similar, both between flowers and between populations. A total of 20 amino acids were identified in the nectar of *E. oliviae* (Table 3). Of these, the most abundant are glutamine (39.68% of the total amount), aspargine (14.58%), and lycine (9.21%). Amino acids constitute 22.91 μmol per ml of nectar; this means that on the average each flower has approximately 5.35 μmol of amino acids.

TABLE 3. Amino acids content in the nectar of *Erythrina oliviae*.

Amino Acids	μmol/ml	Proportion (%)
Alanine	.03	.13
Arginine	.02	.08
Aspargine	3.34	14.58
Aspartic Acid	1.33	5.80
Glutamic Acid	1.62	7.07
Glutamine	9.09	39.68
Glycine	.27	1.18
Hypotaurine	?	?
Histidine	1.05	4.58
Isoleucine	.08	.35
Leucine	.05	.22
Lycine	2.11	9.21
Methionine	1.50	6.55
Ornithine	?	?
Serine	1.31	5.72
Threonine	?	?
Tryptophane	?	?
Tyrosine	.21	.92
Valine	.39	1.70
Phenylalanine	.51	2.23
Total	22.91	100.00

TABLE 4. Number of foraging visits recorded for each species of perching bird taking nectar from *Erythrina oliviae*.

Bird Species	Hours of Observation/Number of Observed Trees		
	El Papayo (4 h/10)*	Chinantla (1 h 30′/5)	Infiernillo (3 h 5′/12)
Icteridae			
Icterus sclateri	36	9	8
I. wagleri	—	3	—
Tangavius aeneus	—	1	—
Troglodytidae			
Campylorhynchus bruneicapillus	8	—	—
C. rufinucha	—	—	4
Picidae			
Centurus hypopolius	8	—	—
Fringillidae			
Pheucticus chrysopeplus	7	—	—
Parulidae			
Unidentified	—	—	1

FLOWER VISITORS

Observations of the flower visitors of *Erythrina oliviae* were made at 27 trees in 3 localities. The approximate total time of observation was 8.5 hours, which included censuses at all hours of the day. A total of 8 species of passerine birds in five families were seen taking nectar (Table 4). In addition, a few individuals of three species of hummingbird (*Amazilia viridifrons* and two unidentified), carpenter bees (*Xylocopa* sp.), and domestic honeybees (*Apis mellifera*) were noted as occasional visitors to the flowers of *E. oliviae*. The perching birds were observed at each study site and were undoubtedly the primary flower visitors. Of these, the orioles, which made 60, 90, and 60%, respectively, of the observed visits to the flowers of the three populations studied, were the primary pollinators. In order to take the nectar, the perching birds approach the flowers of *E. oliviae* in two ways: using the peduncle or a branch as a perch and reaching the flowers from beneath (Fig. 2A), or by perching on the top of inflorescences and inclining the head downwards so as to plunge the beak into the flower (Fig. 2B). The first type of visit seems to be more simple and involves less effort, while the second requires more acrobatic ability. All the perching birds observed taking nectar from *E. oliviae* used the first method, but only the two species of oriole (*Icterus sclateri* and *I. wagleri*) were also observed visiting the flowers in the second way. In the first case the bird's throat or breast is coated with pollen and in the second its crown or forehead. Of the perching birds it was the orioles and, secondarily, the wrens who more easily foraged at the flowers of *E. oliviae*. Since the nectar is concealed by the keel and the wings, it is only accessible to birds with elongated bills. At El Papayo we observed the yellow grosbeak (*Pheucticus chrysopeplus*) destroying the standard and perhaps the keel and

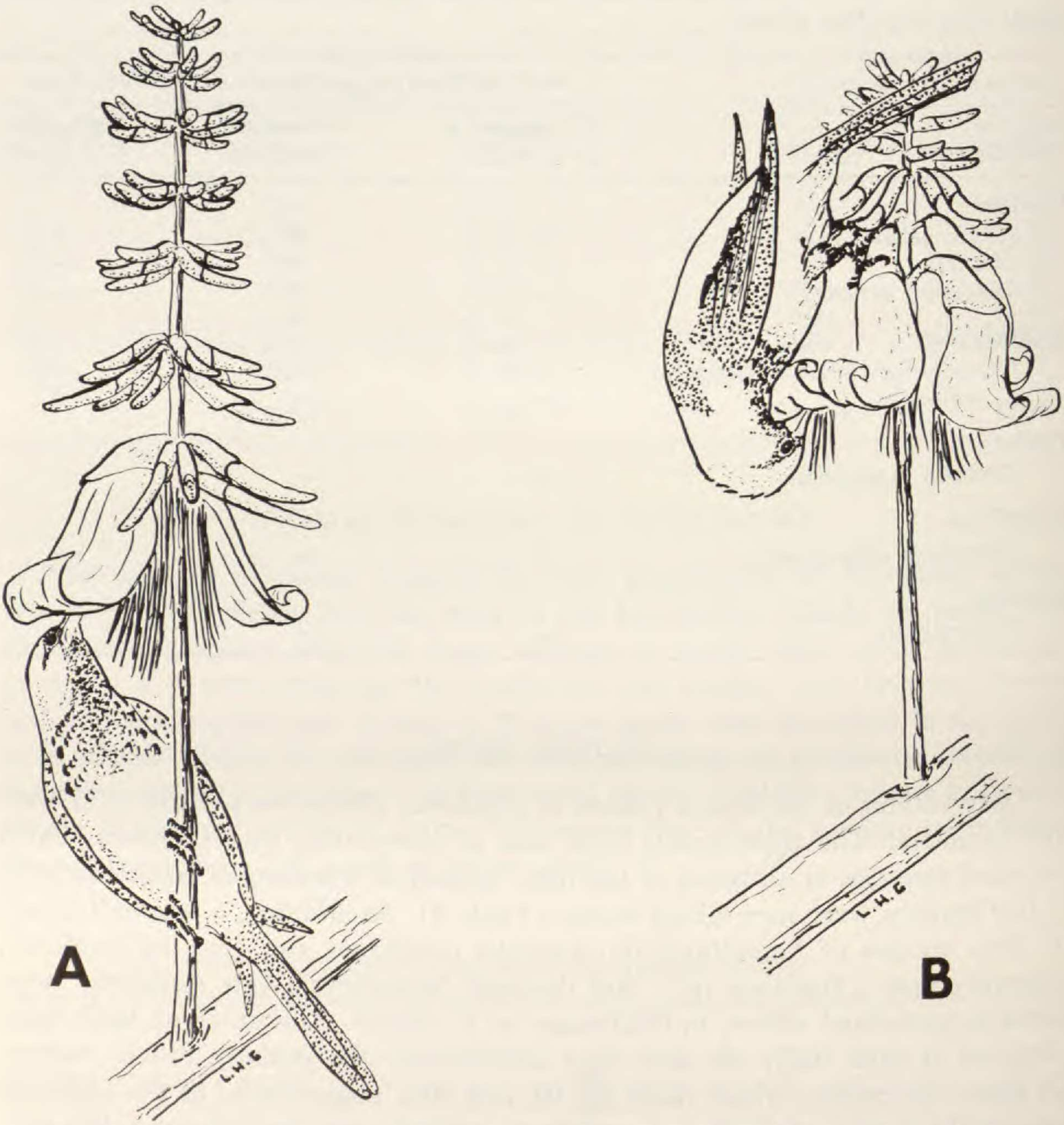

FIGURE 2. The two modalities of foraging visitation of perching birds to flowers of *Erythrina oliviae* (see text).

wings in order to rob the nectar. It is interesting also that while we were at El Papayo the local woodpecker (*Centurus hypopolius*) was a notable visitor of *Erythrina*, but the very abundant woodpecker of the El Infiernillo region (*Centurus chrysogenis*) ignored the flowers of this species completely. In contrast to the passerine birds, hummingbirds were less abundant visitors to the flowers of *E. oliviae* with 3, 8, and 7 visits recorded for the three populations studied. The downwardly directed flowers and the inflorescence structure make foraging by hovering hummingbirds quite difficult. We observed hummingbirds visiting the flowers using the stamens as a perch or piercing the corolla and robbing the nectar. Finally, the carpenter bees and honeybees were observed collecting pollen at the two first hours of the day, after which they disappeared.

Discussion

Excepting the vertical orientation of the inflorescence, all the floral characteristics of *Erythrina oliviae* are consistent with those hypothesized by Cruden & Toledo (1977) as suited to perching-bird pollination. In fact, the hypothesis that oriole-pollinated flowers are of the gaping type and have higher amounts of nectar, lower levels of sugar, and higher numbers of amino acids than the hummingbird-pollinated flowers is confirmed by the results of this paper. Unfortunately, no analysis of ratio of sugars was made in *E. oliviae*, so that it is not possible to test the less "sucrosophilous" condition of the nectar of oriole-pollinated flowers as suggested by the same authors. In relation to the amount of nectar, *E. oliviae* is the species that is known to produce the largest volumes per flower.[4] This may be a direct result of the size of the flower but is also a strategic response of the plant to the drastic climate conditions that prevail within its distributional range. The flowering period of *E. oliviae* coincides with the most severe period of the year when maximal temperatures between 38 and 42°C coincide with extremely low rainfall. Under these conditions water is an extremely scarce resource for animals so that the enormous quantities of nectar provided by *E. oliviae* may attract birds as much by its water content as by its nutritional value (represented by sugars and amino acids). The repeated visits of the birds to the flowers of *E. oliviae* at all hours of the day would indicate this. Twenty amino acids were found in the nectar, including those necessary for growth and maintenance of birds (Fisher, 1972). It is interesting to note that the number of amino acids in *E. oliviae* nectar is higher than that found by Cruden & Toledo (1977) in *E. breviflora* (18 amino acids) and by Baker (1976) in *Jacaratia dolichaula* (J. D. Smith) Woodson (10) and *Carica papaya* L. (9).

It is interesting to note the functions of the keel and wings as nectar containers. Since the flowers are directed to the ground, the keel and wings prevent the nectar from draining off and, in addition, they protect it from desiccation or evaporation induced by the high temperatures of the environment. Moreover, the attractive red color of the inner petals contrasts with the orange of the standard and must operate as a nectar guide to the birds, a very unusual character in ornithophilous flowers (Faegri & van der Pijl, 1971). Finally, the disposition of the keel and wings as a closed container for the nectar must facilitate the visit of orioles and discourage that of other perching birds, since orioles habitually thrust the bill into the closed flower, thereby giving the brushy tongue access to the food (Beecher, 1950).

Erythrina oliviae is the first American perching-bird pollinated species in which the perch has been noted to be vertical. In all described cases of perching-bird pollination in America, which include *Erythrina breviflora* (Cruden & Toledo, 1977), *Bernoullia flammea* Oliver (Toledo, 1977), *Chiranthodendron penta-*

---

[4] Other species of *Erythrina* with large volumes of nectar per flower are two oriole-pollinated species: *E. fusca* (114 μl) (Duncan, unpublished) and *E. breviflora* (64 μl) (Cruden & Toledo, 1977) and one pollinated by hummingbirds, *E. leptorhiza* (42 μl), (Hernández & Toledo, this symposium). However, no species produces more nectar than *E. oliviae*.

dactylon Larreategui (Toledo, 1975), *Combretum farinosum* H.B.K. (Alvarez del Toro, 1963) and *Puya chilensis* Molina (Johow, 1910), birds use horizontal perches in order to obtain the nectar. This particular characteristic of *E. oliviae* probably is a consequence of its African links. In fact, the close resemblance of the flowers of *E. oliviae* to those of some South African species of the genus, and particularly with *E. caffra* Thunberg (Krukoff & Barneby, 1974), suggests that the vertical perch in *E. oliviae* may be a relictual character common to it and relatives now in Africa, where the acrobatic sunbirds are the primary pollinators. In this connection it may be noted that there is much similarity in structure between the inflorescences of *E. oliviae* and *Aloe* spp., an African group of plants adapted to sunbird pollination (Skead, 1967). Thus, *E. oliviae* offers an American example of passerine-bird pollination in which the perch is in a vertical position, whereas *E. breviflora*, which is taxonomically near to the Asiatic sections *Suberosae* Krukoff, *Arborescentes* Krukoff, and *Hypaphorus* (Hasskarl) Krukoff, is of the type where the passerine birds use horizontal perches during the visits to the flowers. Moreover, it is possible to predict from flower structure a similar pattern for two other American species, *E. velutina* and *E. grisebachii*, placed by Krukoff & Barneby (1974) in the predominantly paleotropical sect. *Erythraster*. Similarly, in *E. edulis*, another American species whose flowers are essentially the same as those of *E. breviflora*, an horizontal perch must be expected. This distinction in the passerine-bird pollination (horizontal perch versus vertical perch) should be investigated in the future because it surely is related to behavioral differences of the groups of birds during the foraging. Finally, passerine-bird pollination by a vertical perch seems to be in an evolutionary sequence nearer to pollination by hummingbirds than that of passerine birds using an horizontal perch, since the inflorescence resembles in structure one that is normally hummingbird pollinated.

LITERATURE CITED

ALI, S. A. 1932. Flower-birds and bird-flowers in India. J. Bombay Nat. Hist. Soc. 35: 573–605.

ALVAREZ DEL TORO, M. 1963. La enredadera cepillo, fuente de atracción para las aves. Misc. Ornitológica: Inst. Ci. Art. Chiapas, Méx. pp. 3–5.

BAKER, H. G. 1976. "Mistake pollination as a reproductive system with special reference to the Caricaceae. Pp. 161–169, *in* J. Burley & B. T. Styles (editors), Tropical Trees: Variation, Breeding and Conservation. Linn. Soc. Symp. Ser. No. 2. Academic Press, London.

BEECHER, W. J. 1950. Convergent evolution in the American orioles. Wilson Bull. 62: 51–86.

CRUDEN, R. W. & V. M. TOLEDO. 1977. Oriole pollination of *Erythrina breviflora* (Leguminosae): Evidence for a polytypic view of ornitophily. Pl. Syst. Evol. 126: 393–404.

DOCTERS VAN LEEUWEN, W. M. 1932. Vogel besuch an den Bluten von einigen *Erythrina*-Arten auf Java. Ann. Jard. Bot. Buitenzorg 43: 57–95.

FAEGRI, K., & L. VAN DER PIJL. 1971. The Principles of Pollination Ecology. Pergamon Press, New York.

FISHER, H. 1972. The nutrition of birds. Pp. 431–469, *in* D. S. Farner & J. R. King (editors), Avian Biology. Academic Press, New York.

JOHOW, F. 1910. Sobre algunos casos de ornitofilia en la flora chilena. Estudios de Biología Vegetal I. An. Univ. 126. Santiago de Chile.

KRUKOFF, B. A. & R. P. BARNEBY. 1974. Conspectus of species of the genus *Erythrina*. Lloydia 37: 332–459.

MIRANDA, F. 1947. Estudios sobre la vegetación de México—V. Rasgos de la vegetación en la cuenca del río de las Balsas. Revista Soc. Mex. Hist. Nat. 8: 95–114, figs. 1–27.

PICKENS, A. L. 1931. Some flowers visited by birds. Condor 33: 22–38.
PIJL, L. VAN DER. 1937. Disharmony between Asiatic flower-birds and American bird-flowers. Ann. Jard. Bot. Buitenzorg 48: 17–26.
RAVEN, P. H. 1974. *Erythrina* (Fabaceae): achievements and opportunities. Lloydia 37: 321–331.
———. 1977. *Erythrina* symposium II. *Erythrina* (Fabaceae: Faboidea): Introduction to symposium II. Lloydia 40: 401–406.
SINGH, T. C. 1929. A preliminary note on the pollination of the coral tree (*Erythrina indica* Lamk.) J. Bombay Nat. Hist. Soc. 33: 460–462.
SKEAD, C. J. 1967. The Sunbirds of Southern Africa. A. A. Balkema, Cape Town.
SKUTCH, A. 1954. Life histories of Central American birds. Pacific Coast Avifauna 31.
SNOW, B. K. & D. W. SNOW. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. Auk 88: 291–322.
———. 1972. Feeding niches of hummingbirds in a Trinidad valley. J. Anim. Ecol. 41: 471–485.
STILES, G. F. 1973. Food supply and the annual cycles of the Anna Hummingbird. Univ. Calif. Publ. Zool. 97: 1–116.
TIMKIN, R. L. 1970. Food habits and feeding behavior of the Baltimore Oriole in Costa Rica. Wilson Bull. 82: 184–188.
TOLEDO, V. M. 1974. Observations on the relationship between hummingbirds and *Erythrina* species. Lloydia 37: 482–487.
———. 1975. *Chiranthodendron pentadactylon* Larreategui (Sterculiaceae): una especie polinizada por aves percheras. Bol. Soc. Bot. México 35: 45–52.
———. 1977. Pollination of some rain forest plants by non-hovering birds in Veracruz, México. Biotropica 9: 262–267.